

Invited Review Article

Animal responses to natural disturbance and climate extremes: a review

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ARTICLE INFO

Keywords:
 Behaviour
 Demography
 Disturbance
 Climate extremes
 Impact
 Life history
 Perturbation

ABSTRACT

Natural disturbances, such as droughts, fires or hurricanes, are key drivers of ecological heterogeneity and ecosystem function. The frequency and severity of these episodes is unequivocally expected to increase in the coming decades, through the concerted action of climate change and anthropogenic pressures. This will impose severe challenges for many biota through exposure to rapidly changing conditions never experienced in the preceding millennia. Thus, it is urgently needed to gain a thorough understanding of animal responses and adaptations to disturbances in order to better estimate potential future impacts. Here, we review such adjustments and find that animals may respond to disturbances through changes in: (1) behaviour, such as altered mobility, emigration, resource-switching, refuge use, suspended animation, or biotic interactions; (2) life history traits, such as survival, aging, longevity, recruitment, reproductive restraint, breeding output, phenology and bet-hedging tactics; (3) morphology, such as rapid evolution through size-dependent mortality or facultative metamorphosis; (4) physiology, such as altered body condition, pathogen prevalence and transmission, or adrenocortical modulation of stress responses to emergency conditions; (5) genetic structure, such as changes in frequency of polymorphic variants or diversity-modulation through mortality bottlenecks. Individual-level responses scale up to population and community responses, such as altered density, population dynamics, distribution, local extinction and colonization, or assemblage structure and diversity. Overall, disturbances have pervasive effects on individuals, populations and communities of vertebrates and invertebrates of all realms, biomes, continents and ecosystems. Their rapidly increasing incidence and severity will bring unique study opportunities for researchers and novel, unpredictable challenges for managers, while demanding tougher choices and more proactive crisis-preparation for conservationists, as well as mentality changes for all. Under all conditions, disturbances may soon become the defining signatures of most ecosystems and the dynamic leitmotif of modern ecology.

1. Introduction

Natural disturbances, such as hurricanes, fires or droughts, are major determinants of individual fitness, population dynamics, community structure and ecosystem properties (Sousa, 1984; Pickett and White, 1985). There is growing appreciation that the frequency and severity of these powerful ecological drivers are increasing for two main reasons. First, there is common agreement that climate change is causing an increase in climatic variability and in the occurrence and magnitude of extreme weather events (Easterling et al., 2000; Planton et al., 2008; Rahmstorf and Coumou, 2011; Coumou and Rahmstorf, 2012; Seneviratne et al., 2012; Fig. 1). These episodes are receiving special research attention and media coverage because of their impact on human societies, with high tolls exacted in thousands of human lives, emotional stress and gigantic financial recovery costs (Patz et al., 2005; Strömborg, 2007). In turn, weather extremes may represent or

trigger natural disturbances, such as typhoons or floods. Therefore, most climate models predict increases in the frequency and severity of natural disturbances (e.g. Meehl and Tebaldi, 2004; Seneviratne et al., 2012). Second, such trends are further accelerated by human activities. For example, fire prevention policies often result in larger fuel load accumulation, leading to fires of substantially higher severity and extent (Dodge, 1972). Similarly, heat waves and drought may increase water demands for agriculture, which can lower water tables and trigger even more frequent and severe drought in nearby, more natural ecosystems (e.g. wetlands, Poff et al., 2003; Green et al., 2017).

Throughout their evolutionary history, organisms have responded to these extreme episodes by developing adaptations that allow them to survive or even exploit the disturbance. Such adaptations typically minimize mortality risk during the most vulnerable life stages in order to maximize fitness in temporally fluctuating environments, as postulated by life history theory (Stearns, 1992; Roff, 2002). However, the

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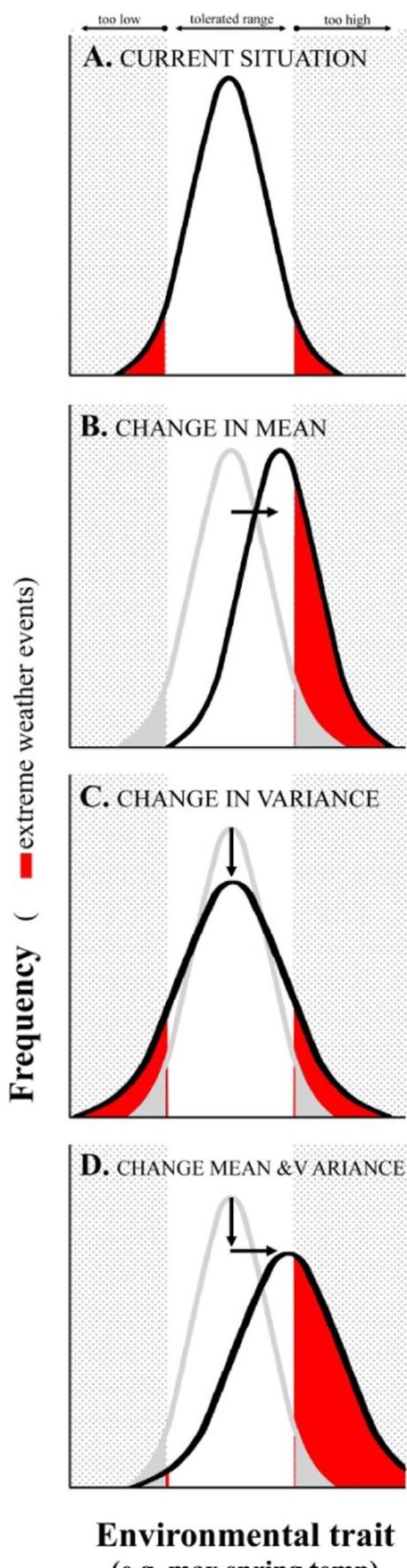


Fig. 1. A gradually shifting climatic mean (such as produced by climate warming, panel B), as well as increased climate or weather variability (panel C), will unavoidably increase the incidence and frequency of climate and weather extremes (panel D), many of which will directly or indirectly trigger natural disturbances, such as droughts, floods, fires or exceptional storms. In the simulated graphs, current climate extremes are highlighted in gray and future extremes in red (re-adapted from Meehl et al., 2000). The increase in extreme conditions and their associated disturbances will be maximum under simultaneous shifts in mean and variance (panel D), a scenario typical of current climate change for many areas of the Earth (Seneviratne et al., 2012).

capability to develop adaptations and survive extreme conditions becomes more difficult as the disturbance becomes increasingly more unpredictable and severe, as shown by both theoretical and empirical studies (e.g. Levins, 1968; Lytle, 2001; Forcada et al., 2008; Lytle et al., 2008; Estay et al., 2014; Bozinovic et al., 2011; Colinet et al., 2015; Roitberg and Mangel, 2016). Thus, the current trends and future forecasts of increased disturbance variability and magnitude may swap the adaptive capability of many organisms by confronting them with conditions never faced before in their recent evolutionary history (Jentsch et al., 2007; Boyce et al., 2006; Parmesan et al., 2000; Vázquez et al., 2017). For example, the Everglades marshes of North America are currently experiencing drier conditions than during the previous 5000 years, as estimated by paleo-ecologists (Nungesser et al., 2015). Such novel settings will likely deteriorate even further in the near future, resulting in formidable fitness challenges for many organisms and a major conservation threat for resource managers.

Given the above, it is ever more urgent and fundamental to increase our knowledge of species responses to disturbance, especially to predict potential future responses by endangered organisms. However, such studies are often logically difficult, knowledge is accumulating slowly, it is often scattered in publications specialized by discipline, realm (aquatic vs terrestrial), biome, taxonomic group, or type of disturbance, typically resulting in research focused on the responses of a restricted number of species. Here, we review the extensive but fragmented literature on animal responses to disturbance. We then attempt to draw some emergent generalities in response dynamics applicable to all disturbances and discuss their conservation implications for building future resilience.

2. Disturbance

We define as disturbance any relatively discrete and unpredictable event in space and time that alters individual performance and the structure of populations, communities or ecosystems through modification of resource availability and the physical environment (modified from Pickett and White, 1985). Disturbances can be generated by geological processes, such as earthquakes and volcanic eruptions, by climate forcings, such as hurricanes, by human action, such as managed fires, or by other biogenic processes, such as outbreaks of pest species (e.g. sudden outbreaks of defoliating insects). They can be punctual or diffuse in extent, they may affect areas from a few square meters (e.g. tree-falls) to whole regions (e.g. droughts) and each type of disturbance may affect cumulatively up to more than 50% of the globe (Walker and Willig, 1999). The agents that generate them may be exogenous, i.e. originate outside the affected site (e.g. a typhoon), or endogenous to the system, such as senescence of a tree causing its fall, thus creating a forest gap. Disturbances are typically characterized by four characteristics: (1) frequency per unit time; (2) magnitude, measured as intensity of the physical force generating the disturbance (e.g. wind speed, or temperature anomaly), or as the severity of its impact on biotas (e.g. number of bleached corals, or felled trees); (3) predictability, the variance in mean interval between successive disturbance events; and (4) areal extent, the area affected by an episode or by multiple episodes within a predetermined period (Sousa, 1984). For most disturbance types, such characteristics are often intercorrelated, with positive covariance between magnitude and extent and negative covariance

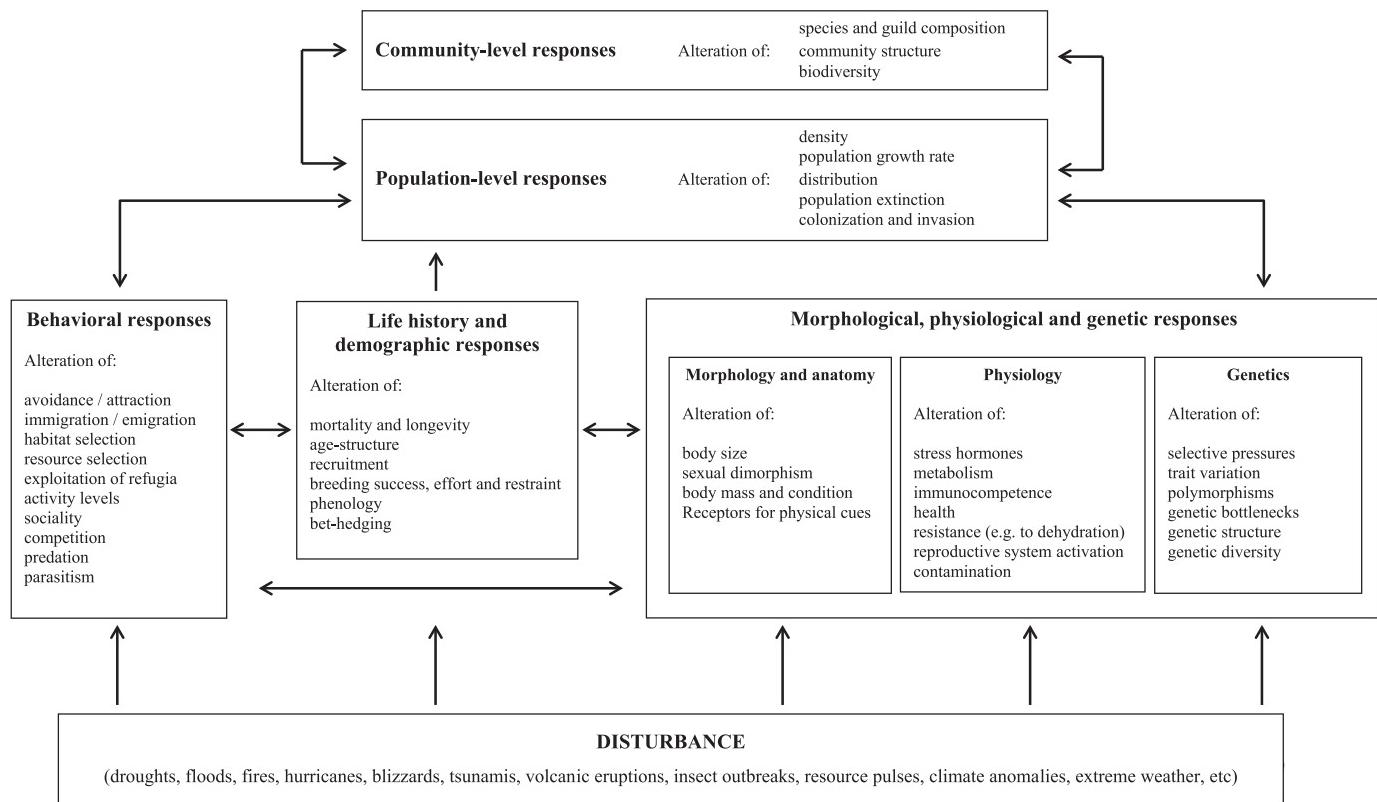


Fig. 2. Animals respond to disturbances through changes in behaviour, life history, demography, morphology, physiology and genetics that scale up to population and community-level properties.

between frequency and magnitude-extent (Walker and Willig, 1999). Thus, for example, large-scale intense disturbances, such as regional droughts, tend to be infrequent, while small-scale ones such as tree-falls are frequent but of low magnitude. However, note that current synergies between climate change and human action may be changing such inherent internal structure of disturbance regimes, as we may expect higher frequencies of high-intensity episodes in the near future (e.g. Meehl and Tebaldi, 2004; Rahmstorf and Coumou, 2011). For example, increasing drought frequency may cause increasing frequencies and extents of high-severity fires, while increasing extremes of precipitation may trigger more frequent, large-scale and severe floods (Seneviratne et al., 2012). These dynamics may represent novel and substantial challenges for local biota.

In this review, we will cover all disturbance types but focus strongly on climate-driven ones, as these are the most likely to increase in the future and generate issues of conservation concern. We will not include: (1) biotic disturbances already covered by the extensive literature on ecological engineering or keystone function, such as dam-building by beavers, or (2) trophic predator-prey relations where the peaks and troughs in prey availability contain a clear element of predictability, such as in rodent cycles. We will instead include non-cyclic outbreaks of rodents or invertebrates, where these are reported as discrete, erratic spikes.

3. Animal responses to disturbance

Disturbances may affect animals through: (1) direct effects, like mortality, displacements and redistributions caused by hurricanes or fires; (2) indirect abiotic effects, mediated by changes in the physical environment, like removal of nesting or foraging substrates (e.g. trees for woodpeckers); and (3) indirect biotic effects, mediated by alteration of the biological environment, such as changes in food availability, predators or pathogens. These effects may impact the performance of

organisms, thus acting as a constraint (e.g. depressing growth or reproduction), or they may promote active strategies and adaptations for coping with unexpected conditions when these emerge (e.g. diapause, emigration, or reproductive restraint). Although previous research has focused heavily on adaptations, it is often difficult or impossible to discriminate between the two mechanisms, which can be seen as interconnected extremes of a continuum. For example, skipping or abandoning reproduction after a disturbance episode may be a passive constraint imposed by poor body condition, but also a strategic decision to curtail the survival costs of breeding under harsh conditions. Simultaneously, the constraint exerted by food-depletion may elevate corticosterone secretion, which may stimulate locomotor activity, leading to dispersal, enhanced foraging and offspring abandonment as an adaptive emergency strategy (Romero and Wingfield, 2016). Furthermore, the morphology of the individuals that will overcome the resource bottleneck and reproduce may dictate the morphological characteristics of the new cohort, representing a powerful pathway of adaptation to the new conditions (e.g. Grant and Grant, 1993). Thus, the overall response to the disturbance will be dictated by the complex interplay of constraints, restraint, active strategic decisions, phenotypic flexibility and micro-evolutionary change (Moreno and Møller, 2011; Vázquez et al., 2017). For this reason, below we define such continuum of responses ranging from active strategies and adaptations to passive constraints as a “response” or “adjustment” by the organism to disturbance.

So defined, animal responses to disturbance have been studied by six main methodologies (Tables A.1–4): (1) short-term comparisons of animal traits before and during or after the disturbance, used as a natural experiment; (2) long-term studies that examine the effect of repeated episodes of disturbance (cycles of recurrent disturbance), again used as a natural experiment; (3) ad hoc experiments that simulate a disturbance (e.g. controlled fires or floods); (4) comparative analyses that examine whether the occurrence of relevant traits across

species is associated with certain disturbance characteristics; (5) investigations of trait-variation among different populations of the same species across gradients of disturbance regimes; (6) studies that compare animal traits post-disturbance between sites directly affected by the episode and nearby control sites not affected by it (e.g. forest gaps created by hurricanes against nearby intact forest sites).

4. Types of responses

Animals can respond to disturbance through changes in behaviour, life history traits, morphology, physiology and genetics and these in turn may bear consequences on population and community dynamics (Fig. 2). Below, we review such responses (Tables A.1–5). Unavoidably, several responses intergrade into each other and can be classified within different non-exclusive categories: for example, stress-driven emigration can be classified as a behavioural, physiological and life history response. Thus, the sub-divisions below are mainly non-exclusive.

4.1. Behavioural responses

Alteration of behaviour is considered the most rapid and efficient form of response to disturbance (Lytle and Poff, 2004). In general, animals may either congregate to exploit the disturbance, flee from it, or remain and respond *in situ* (see Table A.1). Immediate emigration (Table A.1a) is a common response to disturbance by mobile animals inhabiting small wetlands subject to cycles of inundation and complete desiccation, such as many turtles, aquatic snakes or newts (Gibbons et al., 1983; Kennet and Georges, 1990; Siegel et al., 1995; Roe and Georges, 2007; Willson et al., 2006; Kopecky et al., 2010). Fish and water bugs may also migrate laterally within or out of the main riverine channel during high inundation or flash floods and these escape tactics are often mediated by environmental cues that predict the incoming flood, such as increased water velocity or rainfall (Dudley and Matter, 1999; Lytle, 1999; David and Closs, 2002). Migrant birds operate facultative altitudinal movements to lower elevations to escape from unpredictable snowstorms (Hahn et al., 2004), while many animals (e.g. small mammals, invertebrates) flee from fires only to encounter mobile predators that congregate, sometimes from far away, to exploit such vulnerable concentrations of escaping prey (e.g. Smallwood et al., 1982; Tewes, 1984). Similarly, highly mobile, nomadic consumers such as raptors, parakeets or carrion beetles (Silphidae) may track mast years of seed production or carrion-pulses over large areas, sometimes whole regions (Curran and Leighton, 2000; Yang, 2006; Sánchez-Zapata et al., 2007), thus contributing to spatial-averaging of resource pulses (Yang et al., 2008).

In the absence of escape or emigration, animals may still remain in situ but alter patterns of movement in response to disturbance (Table A.1b). For example, movement rates of raptorial snail kites *Rostrhamus sociabilis* increase with drought-mediated food-depletion, while bats foraging ranges may increase 5-fold after hurricanes (Gannon and Willig, 1994; Martin et al., 2006). Such changes are often mediated by opportunistic shifts in habitat use and diet (Table A.1c, d). Thus, flamingos *Phoenicopterus roseus* and snail kites switched to artificially-inundated or other marginal wetlands in years of drought, lizards changed their vertical distribution in forest patches affected by hurricanes, bears became more frugivorous during mast years, and some bats altered their diet from frugivorous to folivorous, or switched foraging habitats from forest to human settlements after cyclones (Takekawa and Beissinger, 1989; Reagan, 1991; Pierson et al., 1996; Béchet et al., 2009).

An alternative response to disturbances, especially destructive ones, is the exploitation of protective refugia (Table A.1e), such as burrowing during floods and fires by invertebrates and small mammals, escaping on trees during floods, the construction of deeper nests or the exploitation of protective sites behind shelters by fish during floods, or the

benefits afforded to frogs by debris accumulated on the forest floor after hurricanes (Erwin and Stasiak, 1979; Palmer et al., 1992; Zulka, 1994; Montgomerie et al., 1996; Woolbright, 1996; David and Closs, 2002). In turn, refuge exploitation may confer clear fitness benefits, such as higher survival of grasshoppers eggs to fire when buried deeper in soil (Branson and Vermeire, 2007), while species of spiders and small mammals that live and den in burrows have higher probabilities of surviving fires than species that live and nest above ground (Riechert and Reeder, 1972; Erwin and Stasiak, 1979; Kaufman et al., 1983; Simons, 1991; Wikars and Schimmel, 2001), providing tight links between behavioural tactics, fitness and demography. These examples show how animal responses may exploit and be shaped by the physical properties of the disturbance medium (e.g. exponential decline of fire-driven temperatures with depth underground).

A further, widespread and efficient way to cope with unfavourable conditions triggered by disturbances is the reduction of activity levels and metabolism through diapause, encystment, cryptobiosis, dormancy or aestivation (Table A.1f). For example, many species of turtles, aquatic snakes and amphibians are known to aestivate in mud or thick vegetation surrounding wetlands when these desiccate completely (e.g. Winne et al., 2006; Kayes et al., 2009), while encystment, dormancy, diapause and cryptobiosis of adults, eggs or cocoons is common in invertebrates of ephemeral habitats (e.g. Hairston and Walton, 1986; Anlauf, 1990; Holmstrup, 2001; Ricci and Caprioli, 2005).

Finally, intraspecific and interspecific interactions are often altered by disturbances. (1) Intraspecifically (Table A.1g), disturbances often reduce food and habitat resources and concentrate individuals in limited refugia, such as drying pools during drought or islands during floods. This increases competition and crowding, often leading to increased fighting and injury, physiological stress and poor body condition (John, 1964; Fitzsimons and Nishimoto, 1995; Covich et al., 2003; MacDonald-Beyers and Labinsky, 2005; Campbell et al., 2008). In some aquatic species, pond desiccation and crowding trigger cannibalism, which in some salamanders is operated through the appearance of a cannibalistic, larger-headed larval morph, i.e. through a polyphenism (Collins and Cheek, 1983; Lannoo and Bachmann, 1984; Pizzatto and Shine, 2008). In addition, disturbance-induced changes in density, distribution and mortality can alter social behaviour. Thus, forest devastation by a hurricane resulted in a protracted period of social disorganization of a monkey population, characterized by more fragmented and unstable social groups, more transient, solitary individuals and lower vocalization rates (Pavelka et al., 2003). Similarly, extreme spates disrupted trout social hierarchies (Sloman et al., 2002), while the congregation pattern of avian social groups responded to severe storms, drought and food pulses (Astheimer et al., 1995; Sánchez-Zapata et al., 2007; Brown and Brown, 2014). (2) Interspecifically (Table A.1h), competition and predation can be alleviated or exacerbated by disturbance. Interaction-relief is usually promoted by the selective removal of the predator or dominant competitor (Doubledee et al., 2003; Thibault and Brown, 2008), while synergistic enhancement usually happens when: (a) resource bottlenecks force species in tighter competition (e.g. “ecological crunch” by drought, Dunham, 1980); (b) habitat change or habitat-switching increases exposure to predators (e.g. when fire removes protective cover for rodents, or when hurricanes and flooding force bats closer to settlements of human hunters or turtles to predation-prone shallow water, Ernst, 1974; Pierson et al., 1996; Morris et al., 2011); or (c) population reduction by the disturbance makes it demographically more vulnerable to predation and vice versa (Schoener et al., 2001). Similarly, disturbances may ameliorate or exacerbate the risk of parasitism and pathogen infection and transmission (see Table A.3e and below).

4.2. Life history and demographic responses

Life history responses to disturbances include alteration of survival, longevity, recruitment, breeding and phenology. Disturbances may

affect life history traits through direct effects, for example by inflicting direct mortality, or through indirect effects mediated by changes in the biotic and abiotic environment, such as breeding failure caused by poor body condition in response to disturbance-driven food depletion.

Mortality is one of the most substantial pressures exerted by disturbances on life history (Table A.2a). In extreme cases, it can remove up to 99% of a population through mass mortality events (Table A.5), while survival can vary by 3-fold on average in response to climate extremes (review in Moreno and Møller, 2011). For example, survival declines were reported for snail kites, finches and salamanders during drought, for dippers during high-floods, for owls and deer during extremely harsh winters, or for bats after hurricanes (Boag and Grant, 1984; Berven, 1995; Pierson et al., 1996; Garrot et al., 2003; Altwegg et al., 2006; Martin et al., 2006; Church et al., 2007). In all these cases, the effects were mediated by a combination of direct killings by the disturbance-medium (e.g. high winds), food depletion, alteration of the physical environment (e.g. retreat sites) and biotic interactions (competition, predation, parasitism). In several cases, mortality disproportionately targeted certain classes of individuals by size, sex, age, or status. Thus, drought and hurricanes affected the survival of younger age classes more than adults in frogs, raptors, monkeys and bats (e.g. Berven, 1995; Pierson et al., 1996; Martin et al., 2006; Pavelka et al., 2003), while drought selectively removed larger female aquatic snakes, thus regulating sexual dimorphism (Winne et al., 2010). Similarly, drought and severe winters disproportionately increased the mortality of older age classes of snail kites and deer, thus accelerating senescence and reducing longevities (Garrot et al., 2003; Reichert et al., 2010; Table A.2b). In turn, selective removal of certain age classes caused long-term changes in population age structure, a phenomenon known as “demographic storage” (Table A.2c): juveniles were often under-represented and sometimes almost completely disappeared from the population, even years after the disturbance (Gannon and Willig, 1994; Pierson et al., 1996; Woolbright, 1996; Altwegg et al., 2006; Pavelka et al., 2003). However, such dynamics were often complex and varied through time after the disturbance episode (Woolbright, 1996; Willig and McGinley, 1999).

Non-breeding individuals often respond to disturbances through acceleration or deceleration of recruitment to the breeding sector of the population (Table A.2d). For example, food pulses triggered by high rainfall induced by El Niño events resulted in massive incorporation of young recruits in breeding populations of Galapagos finches, with opposite trends triggered by droughts (Grant and Grant, 1987). Again, such processes can generate demographic storage through boom-bust dynamics of recruitment, which may erase whole cohorts or over-represent other ones in the future reproductive population. Similar recruitment responses have been reported in fish and snakes and are likely to be commonplace in many taxa, although difficult to study (Table A.2d).

For breeding individuals, disturbances often result in breeding restraint, changes in reproductive effort and performance and, in extreme cases, complete offspring abandonment, as reported by numerous studies (Table A.2e, f). On average, extreme weather events can cause nearly 3-fold variation in breeding rates (Moreno and Møller, 2011). In exceptional cases, disturbances may erase whole multi-species, reproductive assemblages (Schreiber and Schreiber, 1984), or affect entire breeding populations over whole macro-regions. For example, the volcanic eruption of Mount Pinatubo in the Philippines in 1991 triggered a major cooling of the arctic and delayed snowmelt in the following spring through aerosol-cloud circulation, leading to massive breeding failures of millions of waders and waterfowl over the whole circumpolar arctic region (Garter and Boyd, 1992). Such episode was accompanied by complete colony desertions, range displacements, reverse migrations, poor body condition, high proportions of non-breeders in the populations, late laying, low clutch sizes, poor hatching and fledgling success and high predation pressure (Garter and Boyd, 1992 including data from more than 30 populations). On the other hand the

breeding response to disturbance is not obligatorily negative, as demonstrated by increased condor breeding output facilitated by higher carrion availability induced by an El Niño episode in Peru (Wallace and Temple, 1988).

Overall, low breeding effort and iteroparity are predicted by theoretical models as optimal fitness-maximizing strategies under high environmental variability and temporal stochasticity (Charlesworth, 1994; Benton and Grant, 1999). In particular, low breeding effort and restraint are often viewed as active decisions to curtail the survival costs of reproduction when the breeding prospects are poor, as posed by general life history theory (Stearns, 1992; Roff, 2002). In support of these costs, mortality was disproportionately high on salamanders that attempted breeding in drought years (Church et al., 2007). Many disturbances may be ideal bottlenecks to test such tradeoffs.

Often, life history responses are mediated by the opportunistic synchronization of specific stages of the life cycle with particular phases of disturbance development (Table A.2g). Thus, egg deposition and hatching by wetland-dependent animals can be finely tuned on flood dynamics or water recession rates (John, 1963; Nesler et al., 1988; Næsje et al., 1995; Béchet and Johnsson, 2008; Sergio et al., 2011). These responses are often mediated by short-term cues, such as increased water velocities that announce floods and prompt fish spawning in streams and rivers, or receding water levels that promote the acceleration of metamorphosis from aquatic larvae to terrestrial adult forms in amphibians (John, 1963; Nesler et al., 1988; Næsje et al., 1995; Denver, 1997, 1998). In extreme cases, rare disturbances may be key evolutionary drivers of the phenology of major life history stages. For example, despite the well-appreciated breeding advantages of earlier migratory arrival in birds (Newton, 2008), recurrent, massive mortalities of early-arriving individuals caused by extreme cold spells in spring may re-set back the population-level arrival date of migratory birds, as convincingly shown in swallows (Brown and Brown, 2000). These disturbance-mediated risks may constrain the capability of organisms to advance their breeding cycles in response to global warming in order to avoid mismatches with prey-availability (Jonzén et al., 2007). Such concerted action of selective pressures by mean climatic trends and constraints by weather extremes may explain why many species do not seem capable to track current levels of climate change (Visser and Both, 2005; Vázquez et al., 2017).

One commonly reported aspect of disturbances is that the severity of their impact depends heavily on when they happen in relation to the life-stage of the target species. For example, fires may not affect grasshoppers if they coincide with when the population exists mainly as eggs buried deep in the soil, while they can be very destructive at later dates (e.g. Chambers and Samways, 1998; Branson and Vermeire, 2007). Similarly, floods can affect fish spawning, fry emergence and recruitment, but only if they happen in specific periods (John, 1963; Strange et al., 1992; Fausch et al., 2001), while spring storms may be more or less deleterious to songbirds depending on when they happen during the nesting cycle (Wingfield et al., 1983; Wingfield, 1985a, 1985b). In extreme cases, some disturbances may impose constraints on phenology that override any potential coping strategy. For example, avian breeding seasons in the high arctic are often already too short to accommodate further delays caused by unusually late snowmelt (Garter and Boyd, 1992; Martin and Wiebe, 2004). Such environmental thresholds beyond which coping may be difficult are supported by several theoretical models which predict that optimal phenotypic plasticity may be unachievable when the range of environmental conditions becomes too wide (Moreno and Møller, 2011; Estay et al., 2014; Vázquez et al., 2017).

Finally, the unpredictability inherent to many disturbances is likely to select for bet hedging strategies that spread potential risks in space or time to avoid synchronized exposure to adverse conditions (“do not put all your eggs in one basket” strategy). Although bet hedging is difficult to demonstrate (Hopper, 1999), many adjustments seem compatible with it. For example, (1) toads and dragonflies partition their annual

egg capital in several clutches distributed in several ponds differing in likelihood of desiccation (Buschmann, 2002; Schenk et al., 2004); (2) treehole mosquitoes and stoneflies stagger hatching temporally in response to unpredictable water levels, and the extent of staggering increases with the level of environmental fluctuation across populations (Frutiger, 1996; Khatchikian et al., 2009); (3) crickets lay clutches containing a mixture of diapausing and fast-developing eggs in drought-prone soils (Walker, 1980); (4) only a fraction of diapausing larvae of desert bees emerge from pupation in response to erratic rainfall episodes (Danforth, 1999); (5) a portion of salamander and newt larvae can facultatively maintain their aquatic form into adulthood (paedomorphosis) depending on the adversity balance of their aquatic vs terrestrial surroundings (Semlitsch and Wilbur, 1989; Denoël, 2003); (6) avian predators lay eggs asynchronously, resulting in siblings' size-hierarchies, fights and killings that adjust brood size in real time to unpredictable resources, and such level of brood reduction increases with disturbance harshness (Sergio et al., 2011). Overall, the integration of proactive bet hedging and reactive behavioral tactics could facilitate coping arsenals that increase resilience in the face of unpredictable environmental extremes.

4.3. Morphological, physiological and genetic responses

Morphological changes in response to disturbance have been repeatedly demonstrated, usually as end-products of disproportionate mortality affecting certain portions of the size gradient (Table A.3a). In the most famous textbook example of Darwin's finches (Grant and Grant, 1993, 2003), drought increased seed hardness and the mortality of these granivorous finches selectively targeted smaller individuals with weaker beaks less capable to crack the hard seeds. However, these smaller individuals were advantaged over larger ones during subsequent El Niño years of intense rainfall when seeds became smaller again, so that body and beak size were subject to oscillating selection induced by the alternation of major disturbances. In other cases, the lower food availability caused by drought disfavoured larger individuals because of their higher energetic demands (Bryant and Jones, 1995; Winne et al., 2010), while extreme cold spells and storms almost erased smaller individuals from the population through mass mortality (Johnston et al., 1972; Brown and Brown, 1998). In some studies, disturbance-induced size-mortality targeted the sexes differentially, thus shaping sexual dimorphism (Johnston et al., 1972; Winne et al., 2010). In other cases, morphology is not only shaped by mortality but also changes individually in a longitudinal manner: marine iguanas can reabsorb bone tissue and shrink in size to better survive famine during El Niño years, while salamanders and newts can facultatively metamorphose into terrestrial adults or retain their aquatic larval form into adulthood depending on drought (Semlitsch and Wilbur, 1989; Denoël, 2003; Wikelski and Thom, 2000).

Independently of size and morphology, body mass and condition frequently respond to disturbances (several examples in Table A.3b). Storage or mobilization of fat reserves during disturbance-induced resources pulses or bottlenecks is the most likely modulator of such changes in condition (e.g. Wingfield et al., 1983; Wingfield, 1985a, 1985b; Astheimer et al., 1995).

Responses to disturbances are often mediated by physiological adjustments which modulate coping mechanisms (Romero and Wingfield, 2016; Table A.3c). For example, when disturbances cause allostatic overload, vertebrates may enter an emergency state through activation of the hypothalamic-pituitary-adrenal axis (HPA), which results in elevated levels of circulating glucocorticoid hormones (cortisol and corticosterone). The latter controls key coping mechanisms and behaviours in emergency situations, such as glucose mobilization, escape, emigration, foraging, or abandonment of breeding activities. Thus, elevated glucocorticoids levels have been reported in pythons and quails facing experimentally simulated drought (Cain and Lien, 1985; Dupoué et al., 2014), in marine iguanas and seabirds during El Niño

famines (Wingfield et al., 1999; Romero and Wikelski, 2001), in alligators in response to wetland salinization caused by an anomalous hurricane-induced tidal surge followed by drought (Lance et al., 2010), and in passerines and seabirds confronted with prolonged storms (Wingfield, 1985a,b; Wingfield et al., 1983). In some of these studies, elevation of corticosterone levels paralleled declines in body condition, depletion of fat reserves, inhibition of breeding and offspring abandonment (Wingfield et al., 1983; Cain and Lien, 1985; Wingfield, 1985a,b; Smith et al., 1994; Astheimer et al., 1995; Wingfield et al., 1999), supporting a link between disturbance-induced stress and hormonal modulation of coping behaviours (e.g. breeding abandonment in favour of a "survival mode"). In a textbook case, increased secretion of corticosterone and thyroid hormones mediated the escape of a toad from experimentally desiccating ponds by accelerating metamorphosis to the terrestrial adult form (Denver, 1997, 1998).

Physiology and anatomy may further mediate fine-scale adaptations that enable disturbance resilience or exploitation (Table A.3d). For example, physiological resistance to dehydration in response to unpredictable drought is attained through decreased metabolism, water reabsorption from the urinary bladder, osmolality, nitrogen excretion through urea-conversion and increased glycolysis and gluconeogenesis during sustained animation (e.g. Peterson, 1996; Saha et al., 2001; Ligon and Peterson, 2002; Ragland et al., 2010). Similarly, some fishes avoid the metabolic demands of sustained swimming during high floods by anchoring themselves to the substrate through mouth suction (Ward et al., 2003), while pyrophilous beetles can detect fires from several kilometres away through thoracic pit organs sensitive to infrared radiation and specialized smoke-detecting chemoreceptors in their antennae (Schütz et al., 1999). Finally, finches of arid areas with unpredictable resources maintain their reproductive system partially activated during the non-breeding drought periods, so as to enable opportunistic fast breeding in response to sudden rainfall (Perfito et al., 2007).

The extreme conditions and behavioural responses (e.g. displacement to new habitats) provoked by disturbances often expose animals to parasitic and pathogenic insults to the immune system (Table A.3e). In particular, disturbances can affect health in three ways: (1) they may redistribute pathogens, parasites and pollutants through changes in air and water circulation, or provide conditions that favour or disfavour their transmission or their biotic vectors (Epstein, 2001; Epstein and Defilippo, 2001; Ivers and Ryan, 2006). For example, multi-decadal droughts in a portion of the African Sahel locally erased malaria through the virtual extinction of its mosquito vector (Mouchet et al., 1996), while temperature extremes can modulate the speed and intensity of malaria infection (Paaijmans et al., 2010). (2) They may affect overall body condition and the immune system, thus altering individual susceptibility to disease. For example, drought deteriorated the immune responsiveness and body condition of three songbirds, resulting in higher mortality (Fair and Whitaker, 2008). Finally, (3) they may alter local socio-ecological conditions in ways that affect disease transmission. For example, crowding due to receding water levels increased Chytridiomycosis infection in a frog population (Longo et al., 2010). As a consequence, disturbances often exaggerate or attenuate health insults (Table A.3e). Thus, the alternation of high flood and drought modulated the rate of river fish parasitism by trematodes (Janovy et al., 1997), a 100-year exceptional flood recirculated PCB toxic chemicals stored in lake sediments, leading to widespread contamination, deformities and breeding failure by terns (Ludwig et al., 1993), while drought exacerbated the impact of Hg-contamination, leading to hepatic, renal, neural, thyroid and immune system disturbances in herons (e.g. inflammation, oxidative stress; Hoffman et al., 2009). In unfortunate cases, human pollution may act as a punctual, unpredictable disturbance itself. For example, a major oil spill in the Galápagos caused massive mortality of marine iguanas through starvation caused by erasing the endosymbiotic hindgut bacteria essential for digestion (Romero and Wikelski, 2002). Note that all the health

impacts of disturbances here described have also been reported in humans, which could be expected to be more buffered from environmental perturbation than wild animals (e.g. Mouchet et al., 1996; Epstein, 2001; Epstein and Defilippo, 2001; Ivers and Ryan, 2006). Furthermore, such effects can be subtle and carry over into the next generation (e.g. King et al., 2012).

Finally, disturbances can cause genetic responses in three main ways (Table A.3f): (1) they may impose selective pressures on traits that are genetically heritable. For example, disturbance-driven oscillating selection superimposed on morphological trait heritability shaped the beak and body size of Darwin's finches (Grant and Grant, 2003). (2) They may modulate genetic polymorphisms that underlie adaptive responses to perturbations, such as paedomorphosis (Semlitsch and Wilbur, 1989). For example, substrate blackening by fire acted on the colour polymorphism of a grasshopper inducing rapid increases in its black morph, genetically favoured by improved camouflage (Forsman et al., 2011). (3) Disturbances can alter dispersal, isolation and distribution or cause population crashes, leading to changes in genetic structure and diversity, such as the genetic bottlenecks caused in snails, birds, or iguanas by drought, hurricanes, earthquakes and El Niño famines (Steinfartz et al., 2007; Evanno et al., 2009; Szczys et al., 2012), or the expansion of genetic diversity after a hurricane that probably assisted bat dispersal (Fleming and Murray, 2009).

4.4. Population and community responses

Disturbance-driven changes in the pattern of natality, mortality and dispersal (Tables A.1, A.2 and A.5) unavoidably translated into population-level growth rates, leading to population increases or declines and ultimately regulating local density. In many studies, population growth, trend and density covaried with disturbances (Table A.4a) through direct effects (e.g. mass mortality, Table A.5), or indirect effects, such as variation in adult survival (e.g. Beissinger, 2008), or resource limitation. For example, fire may maintain optimal habitat and abundant food for some birds and butterflies (Breininger et al., 1995; Rota et al., 2014; McElderry et al., 2015), while a single hurricane removed 87% of 1765 nesting cavities of an endangered woodpecker (known to be limited by nest availability, and taking up to one year to excavate a single cavity; Hooper et al., 1990).

Density-adjustments may be complemented by changes in distribution following disturbance at several spatial scales (Table A.4b), from local nesting or foraging habitat-switching (Takekawa and Beissinger, 1989; Bennets et al., 2002; Beerens et al., 2015), to larger shifts in regional range (Shilton et al., 2008). In extreme cases, distribution may change radically as a result of local extinction or invasion (Table A.4c, d). Population extinction was often the result of: (1) repeated blows or prolonged action by the same disturbance (Ehrlich et al., 1980; Mouchet et al., 1996; Pounds et al., 1999), or (2) synergistic effects of multiple disturbances (Spiller et al., 1998; Schoener et al., 2001). On the other hand, colonization and invasion can be: (1) assisted by disturbances when these breach physical barriers (Johnston and Purkis, 2015; Frank et al., 2013) or remove dominant competitors (Thibault and Brown, 2008); or (2) impeded by disturbances, as occurs in many streams when high floods disproportionately displace non-native fauna (Fausch et al., 2001; Costelloe et al., 2010; Pintor and Sih, 2011) or in wetlands where droughts arrest the spread of invasive species (e.g. Díaz-Paniagua et al., 2014).

Finally, disturbances can alter interspecific interactions (Table A.1h) and produce differential effects on species or guilds, leading to changes in community structure and biodiversity (Table A.4e). For example, fires, hurricanes and heatwaves produced different, even opposed impacts on different guilds of forest arthropods (Moretti et al., 2004; Rouault et al., 2006; Shiels et al., 2014), while a two-hour storm reorganized a whole rodent community through massive removal of a dominant competitor (Thibault and Brown, 2008).

5. Emergent generalities

The above overview has shown an extremely wide array of anatomical, morphological, genetical, physiological, behavioural, demographical and life history responses to disturbance that scale up from individual-level to population and community adjustments. A common denominator to most studies is the rapidity, intensity and dynamism of environmental change experienced by model organisms, which often induce evolutionary bottlenecks, mimic extreme conditions like those experienced at the border of distribution ranges, and lend unique opportunities for natural experiments to study adaptation and resilience to global change. In many ecosystems, such bottlenecks make disturbance the most fundamental modulator of trait design, individual fitness, population dynamics and community structure, even when it is a rare event (e.g. Brown and Brown, 2000; Grant and Grant, 2003; Martin et al., 2008; Thibault and Brown, 2008). Overall, given the heterogeneity of conditions and responses generated, it is difficult to synthesize a generally-applicable scheme of response trajectories. However, some aspects emerge recurrently enough from disparate studies to enable us to draw the following main generalities.

- (1) **Differential effects:** the same disturbance may produce profoundly different effects on different species (e.g. Smith, 1982; Moretti et al., 2004; Rouault et al., 2006; Fontaine and Kennedy, 2012) and coping efficiency is often promoted by certain population features, such as initial size and viability, by certain behavioural characteristics, such as mobility, opportunism and guild affiliation, or by certain life history traits, such as iteroparity and high longevity (e.g. Charlesworth, 1994; Willig and McGinley, 1999; Parmesan et al., 2000; Piessens et al., 2009). The latter enables learning through experience from multiple disturbance episodes, and exploitation of trade-offs, such as breeding abstention for survival enhancement (e.g. Church et al., 2007). Furthermore, some species may be pre-adapted to cope with unpredictable perturbations (e.g. through asynchronous hatching or aestivation), because these are already integral to their ecosystems (e.g. drought in intermittent streams of arid environments). Thus, there is moderate room for predicting species or populations potentially at risk.
- (2) **Cumulative response:** each species is likely to respond to disturbance through an integrated strategy of coordinated responses. For example, pyrophilous beetles use specialized chemoreceptors to detect fires from large distances, they reach them from up to 50 km away through low wing-loading and large flight muscles, leading to patch colonization and abandonment that govern their local abundance and diversity through metapopulation dynamics (Wikars, 1997; Schütz et al., 1999; Wikars and Schimmel, 2001; Moretti et al., 2004; Ranius et al., 2014). The cumulative synergy of such responses will determine eventual coping success, underlying the necessity of comprehensive studies.
- (3) **Thresholds:** in most cases, there will be thresholds of disturbance frequency and severity beyond which coping becomes unattainable (e.g. Martin and Wiebe, 2004), leading to mass mortalities and population crashes or extinction. Thus, the fact that so many responses are possible (Table A.1–4) should not be equated with frequent absence of impact. In extreme cases, thresholds may impose regime shifts. For example, breaching of certain temperature thresholds may trigger regional-level insect outbreaks, while flooding of a sufficient magnitude can wipe out a dominant competitor, permanently reorganizing a rodent assemblage in just two hours (Raffa et al., 2008; Thibault and Brown, 2008).
- (4) **Temporal dynamics:** responses to disturbances change with the time passed since the perturbation (Willig and McGinley, 1999), so that impact assessments should control for temporal dynamics. Furthermore, different species may show profoundly different recovery trajectories post-disturbance. For example, populations of two bat species had fully recovered within two years of a hurricane, while a

- third one was still 30% of its original size after three years (Gannon and Willig, 1994). In some cases, disturbance effects can be extremely long-lasting, such as the continued avoidance by caribou of patches burnt 50 years before, induced by the slow recovery of their lichen food (Schaefer and Pruitt, 1991).
- (5) **Importance of timing:** the timing of a disturbance relative to the annual life stage of the target species is often a key determinant of its effect. For example, extreme storms had a stronger impact on songbirds when they coincided with the energy-demanding offspring-raising period compared to pre-incubation, while floods triggered fish spawning only when they happened in specific periods of the year (e.g. John, 1963; Wingfield et al., 1983; Wingfield, 1985a,b; Strange et al., 1992; Fausch et al., 2001).
- (6) **Synergistic impacts and human contingencies:** some disturbances can be casually overlaid on other ones or can trigger other disturbances, leading to amplified effects (Breininger et al., 1999; Gaston et al., 2002; Lance et al., 2010). For example, hurricanes are often accompanied by extreme tidal surges, volcanic eruptions can cause climate extremes, while droughts can trigger fires. Similarly, anthropogenic pressures often accentuate disturbance severity and vice versa. For example, habitat fragmentation increased the risk of drought-mediated population extinction for butterflies, hunting by humans amplified the mortality imparted on bats by a cyclone, while floods and droughts triggered and accentuated the impact of toxic chemicals on wetland birds (Ludwig et al., 1993; Pierson et al., 1996; Hoffman et al., 2009; Piessens et al., 2009). In many cases, the coping mechanisms that would easily ensure resilience are compromised by human contingencies. For example, many aquatic amphibians and reptiles can overcome drought by moving opportunistically through a network of permanent and temporary wetlands, but human development increasingly precludes such movements (e.g. Roe and Georges, 2007). The main problem caused by all the above synergies is that their cumulative effects are difficult to predict and that the amplified severity may more unexpectedly breach the thresholds that trigger regime shifts. For example, the synergy of extreme temperatures and forestry monocultural management increases the likelihood of regional-level, catastrophic outbreaks of insect pests (Raffa et al., 2008).
- (7) **Domino effects:** the mobility, mass mortality, indirect effects and interactions induced by disturbances can cause massive displacements of organisms to other areas, or radically change socio-environmental settings in situ. This will frequently cause important domino effects on organisms not initially affected by the disturbance, an aspect that has received very little attention.

6. Conclusions: prospects and applications

Climate records and forecasts unequivocally indicate that many disturbances are already increasing in frequency and severity and will continue to do so throughout the coming century (Fig. 1). Droughts, heat waves, dust storms, exceptional precipitation events and landslides will all become more common and severe over the coming decades over large regions of the earth (Easterling et al., 2000; Meehl and Tebaldi, 2004; Planton et al., 2008; Rahmstorf and Coumou, 2011; Coumou and Rahmstorf, 2012; Seneviratne et al., 2012). For example, river flow is predicted to decline by 25–45% all over the globe by 2050, with a 2–3 fold increase in the frequency of severely-low flows in Europe, causing many large rivers to become intermittent, temporary water bodies (Arnell, 2003). Meanwhile, mounting anthropogenic pressures are increasingly amplifying disturbance effects on biota, as in the recent crisis to save Indonesian orangutans from the 2-million ha forest devastation caused by unprecedented fires triggered by a lethal synergy of poor land management and El Niño conditions (Drake, 2015). Thus, changes in disturbance regimes and their ecological consequences are likely to become the new millennium leitmotif for ecology, conservation, and even human development and economics. In this scenario, improving

our knowledge of wildlife responses to disturbance will be increasingly important, also because some of these responses will have direct impacts on human communities. For example, prey scarcity caused by drought triggered an upsurge in killings of humans by lions *Panthera leo* in western India (Saberwal et al., 1994).

Given the above, some changes in scientific and management mentality will be important: (1) as disturbances may become an “everyday occurrence”, they should not be treated anymore as rare, exceptional events, but rather planned as likely contingencies even within short conservation or research projects (e.g. three years). (2) Their effects should not be considered negative by default, switching from a mentality of “impacts” to a mentality of “responses”. For example, mass mortality events can be shocking, but in some cases they can also be powerful mediators of rapid adaptation to new regimes (e.g. morphological changes). Similarly, many species have evolved to exploit the special conditions or resource pulses offered by disturbances (e.g. Breininger et al., 1995; Lytle and Poff, 2004; Yang et al., 2008; Rota et al., 2014) and most perturbations will disfavour some species but also benefit others (Colinet et al., 2015). In many cases, compromises will be obligatory and tough choices will have to be made about which species to protect through management (e.g. Curnutt et al., 2000). (3) At the same time, while animals have adapted to disturbances for millions of years (e.g. Hembree, 2009; Romero and Wingfield, 2016), current changes in regimes are occurring over timescales of decades. Thus, for species disfavoured by the perturbation, return intervals may become too short to allow recovery before the next episode and the likelihood that different disturbances will coincide will unavoidably increase (Fig. 3). As we have seen, population extinction is often linked to such sequential or simultaneous blows by multiple shocks. (4) Uncertainty, variability and stochasticity will become more conceptually important because disturbances insert spatio-temporal heterogeneity in ecosystems thus generating complex boom and bust dynamics overlaid on background gradual changes (e.g. Thibault and Brown, 2008).

From an applied point of view, forecasting impacts will be difficult for multiple reasons. First, disturbance regimes are changing rapidly, thus generating novel conditions. Second, it is usually difficult to know a priori which combination of responses will be adopted by each species and how these will feed to population growth, while synergies, interactions and indirect effects may generate subtle and unexpected outcomes. Given the unavoidable uncertainty, it will be fundamental more than ever to accelerate any preliminary work that will enable to face potential bottlenecks in the safest and most informed way, especially for threatened species. This could be attained by: (1) ensuring a large enough population size to absorb potential shocks; (2) increasing intra- and inter-population connectivity and corridors, to enable rescue effects and escape tactics for mobile species; (3) improve knowledge on demographic functioning and elasticities to identify parameters most sensitive to impacts; and (4) whenever possible, analyse responses to past disturbances to estimate potential future adjustments.

Finally, from the research point of view, disturbances represent unique settings for scientific insight. To optimize such opportunities and best complement past studies, new research should strive for: (1) long-term studies, capable to sample repeated disturbance episodes and take advantage of data from before and after each perturbation; (2) holistic, multi-disciplinary and collaborative endeavours, capable to integrate the diversity of fields pertinent to disturbances, such as physiology, genetics, anatomy, morphology, demography, remote sensing or landscape ecology; (3) comprehensive approaches, that examine the combined effect of multiple responses through time, rather than a single response which may be buffered by other parameters; (4) integration of complementary analyses, which incorporate long-term data and ad hoc experimentation or multi-site BACI (Before-After-Control-Impact) designs; (5) improved development of theoretical models (e.g. on life history evolution in stochastic environments); (6) higher reporting of zero-impacts, which would enable to identify species less at risk than others and a more solid implementation of quantitative meta-analyses;

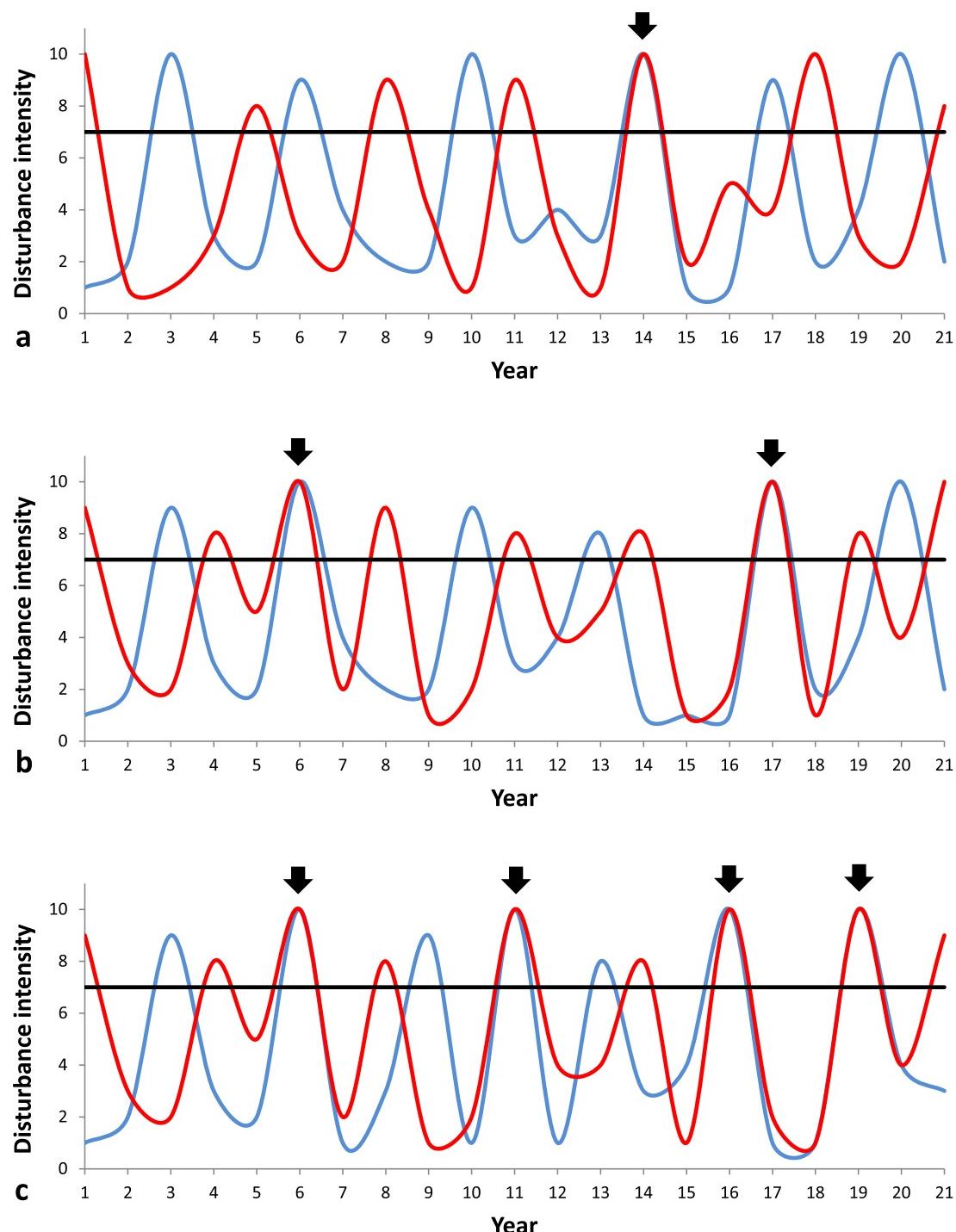


Fig. 3. Simulation of temporal coincidence of two types of disturbances (red and blue, e.g. drought and fire) under different regimes of disturbance frequency. In panel a, the return interval (years between two successive episodes of the same disturbance) is 3–4 years (arranged in a random sequence) for both disturbances, which start out of phase with each other: the two disturbances coincide once in 20 years (highlighted by a black arrow). In panel b, the return interval is still 3–4 years for the blue disturbance (e.g. drought) but has decreased to 2–3 years for the red one (e.g. fire): the two disturbances now coincide twice in 20 years. In panel c, the return interval has declined to 2–3 years for both disturbances: they will now coincide four times in 20 years. As the frequency of one or both disturbances increases, so does the probability of their simultaneous occurrence. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(7) utilization of emergent technologies, such as bio-logging, that may allow unprecedented long-term monitoring of behavioural, physiological and demographic performance at the individual level, even during unfeasible research conditions (e.g. during volcanic eruptions, Alarcón et al., 2016); (8) development and exploitation of new experimental approaches and analytical tools for dealing with variability and uncertainty (e.g. Kaatz et al., 2005; Boyce et al., 2006; Prates et al., 2010;

Kingsolver and Woods, 2016; Thompson et al., 2013) and implementation of quantitative forecasting tools, such as the simulation of Everglades inundation dynamics under different scenarios of management and climate warming (Fennema et al., 1994; Curnutt et al., 2000); (9) measurement of dynamic attributes (survival, performance) that complement static attributes (occurrence, biodiversity), so as to gain insight into mechanisms and not only outcome patterns; (10) increased

focus on synergies, human contingencies and regimes rather than evaluations of a single episode, enabling analysis of disturbance sequences: for example, the effect of a drought year may be different if it follows a flood year versus another drought year.

In conclusion, disturbances and their changing regimes can be ideal opportunities for scientists, intriguing challenges for modellers, puzzling uncertainties for the manager, health hazards for developers and potential nightmares for conservationists. Whatever the approach, they may soon become the defining signatures of most ecosystems and the dynamic leitmotif of modern ecology.

Acknowledgements

We thank Dr. Marret-Davies and two anonymous reviewers for constructive comments on a previous draft of the manuscript. This work was supported by the Ministerio de Economía y Competitividad (grant CGL2015-69445-P) and by the Junta de Andalucía (grant RNM-7307).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gloplacha.2017.10.009>.

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